

*Field Studies.*— $F_1$  plants of the cross Federation  $\times$  Kenya 744 showed slight development of rust in the field and they were classed as moderately resistant. Kenya 744 showed complete freedom from stem rust and Federation was susceptible.

Two hundred and sixty-eight  $F_3$  lines of the Federation  $\times$  Kenya 744 cross were also grown in the field. All the four Australian races of stem rust were present and the lines were classified as resistant to moderately resistant, segregating and susceptible. Table 5 contains the data on the  $F_3$  lines.

TABLE 5.  
*Classification of  $F_3$  Lines of the Cross Federation  $\times$  Kenya 744 for Their Reaction to Stem Rust in the Field.*

		Reaction to Stem Rust in the Field.				
		Resistant.	Resistant to Moderately Resistant.	Segregating.	Susceptible.	Total.
Parents ..	Kenya 744	—	—	Federation	—	
$F_3$ lines ..	—	78	134	56	268	

P value for 1 : 2 : 1 ratio lies between 0.10 and 0.20.

The field data also indicate the presence of a single major factor for resistance in Kenya 744. The resistance was partially dominant and appears to be influenced by modifying genes. Since 744 is a very early variety escapes can probably account for the larger number of resistant lines as compared to the susceptible ones. Of the 268 lines 151 were tested in the glasshouse with race 222AB and Table 6 shows relationship between the seedling and field reaction which is fairly satisfactory.

TABLE 6.  
*Relationship of the Seedling Reaction of Federation  $\times$  Kenya 744  $F_3$  Lines to Their Reaction in the Field.*

	Seedling Reaction to Race 222AB.			
	Resistant to Semi-resistant.	Segregating.	Susceptible.	Total.
Reaction to Races 126, 126B, 222AB, 222BB in the field :				
Resistant to moderately resistant .. .. .	41	6	—	47
Segregating R & S, or R- & S. . . . .	4	56	10	70
Susceptible .. .. .	—	4	30	34
Total .. .. .	45	66	40	151

*Relationship between races.*— $F_3$  lines of the cross Federation  $\times$  Kenya 744, with known reactions to race 222AB, were tested in the  $F_4$  generation against races 126, 126B and 222BB. Twenty-nine lines which were homozygous resistant to race 222AB, bred true for their resistance against the other three races. Another 22  $F_3$  lines homozygous susceptible to race 222AB also showed the same breeding behaviour against the other races. From this it can be concluded that the same gene in Kenya 744 was responsible for resistance to the four races of stem rust.

*Studies with race 38.*—Preliminary tests made on  $F_3$  lines of the cross Federation  $\times$  Kenya 744 did not show strong correlation between reactions to race 38 and race 222AB.  $F_3$ s of the cross Chinese White  $\times$  Kenya 744 were tested with race 38 to study the mode

of inheritance of resistance. The data in Table 7 show that Kenya 744 has two factors for resistance to race 38. One of these factors appears to be only partially dominant. The plants showing an intermediate type of reaction were grouped with the resistant and semi-resistant class when interpreting the data. The goodness of fit was not very satisfactory, probably because some of the plants classified as intermediate for their reaction to race 38 are genotypically susceptible. The data on  $F_1$  lines included in the same table confirm the presence of two factors in Kenya 744.

TABLE 7.

*Reactions of  $F_2$ s of the Cross Chinese White  $\times$  Kenya 744, and  $F_2$ s of the Cross Federation  $\times$  Kenya 744 to Stem Rust Race 38.*

	Reactions to Race 38.				
	Resistant to Semi-resistant.	Intermediate.	Segregating.	Susceptible.	Total.
Parents of $F_2$ s . . . . .	Kenya 744	—	—	Chinese White	—
Chinese White $\times$ Kenya 744 $F_2$ s	708	36	—	36	780
Parents of $F_2$ s . . . . .	Kenya 744	—	—	Federation	—
Federation $\times$ Kenya 744 $F_2$ s . .	55	—	68	6	129

P value for 15 : 1 ratio for  $F_2$  data lies between 0.05 and 0.10.—P value for 7 : 8 : 1 ratio for  $F_1$  data lies between 0.50 and 0.70.

The reactions of 178 randomly selected  $F_3$  and  $F_4$  lines of Federation  $\times$  Kenya 744 cross to race 38 and race 222AB are compared in Table 8.

These data show that one of the two factors in Kenya 744 which give resistance to race 38, is the same as the one giving resistance against race 222AB. Figures within brackets in Table 8 indicate the lines which show reactions not expected on the basis of

TABLE 8.

*Distribution of 178 Lines of the Cross Federation  $\times$  Kenya 744 for Their Reaction to Race 38 and Race 222AB.*

	Reaction to Race 38.			
	Resistant to Semi-resistant.	Segregating.	Susceptible.	Total.
Reaction to race 222AB :				
Resistant to semi-resistant	51	(2)	—	53
Segregating . . . . .	24	57	(1)	82
Susceptible . . . . .	8	27	8	43
Total . . . . .	83	86	9	178

this hypothesis. This is a minor discrepancy and could happen by chance. If the three families showing the unexpected behaviour are disregarded, the reactions of the rest of the lines (51:24:57:8:27:8) can be fitted with expected ratio of 4:2:6:1:2:1 on the basis of preceding hypothesis. The P value for the goodness of fit lies between 0.30 and 0.50 which is fairly satisfactory.

It is of some interest to find the presence of two factors in Kenya 744 against race 38. Only one of them is effective against Australian rusts. Several other varieties, for example, Bencubbin, Ford, Gular and Mentana, which are susceptible to stem rust in Australia show resistance to race 38. Work is in hand at present to relate the resistance of these varieties to race 38 with that of Kenya 744.

*Inheritance of the resistance of Kenya 117A.*

*Glasshouse studies with race 222AB.*—6  $F_1$  plants of the cross Federation  $\times$  Kenya 117A were tested with race 222AB and were found to be almost as resistant as Kenya 117A.

Athwal (1953) reported that reactions of  $F_2$  segregates from crosses involving Kenya 117A were difficult to read and the heterozygous plants showed an intermediate type of

TABLE 9.  
*Reactions of  $F_2s$ ,  $F_3s$  and  $F_4s$  of the Cross Federation  $\times$  Kenya 117A to Race 222AB.*

	Reactions to Race 222AB.			
	Resistant or Semi-resistant.	Segregating.	Susceptible.	Total.
	Kenya 117A	—	Federation	—
$F_2s$	407	—	138	545
$F_3s$	24	49	23	96
$F_4s$	15	45	22	82

P value for 3 : 1 ratio for the  $F_2$  data lies between 0.80 and 0.90.—P value for 1 : 2 : 1 ratio for the  $F_2$  data lies between 0.95 and 0.98.—P value for 1 : 2 : 1 ratio for the  $F_4$  data lies between 0.30 and 0.50.

reaction. With race 222AB, however, the segregation was clear cut and heterozygous  $F_2$  plants were indistinguishable in their reactions from homozygous plants. The data on  $F_2s$ ,  $F_3s$  and  $F_4s$  of the cross Federation  $\times$  Kenya 117A are presented in Table 9.

$F_2$  data indicate the presence of a single dominant factor for seedling resistance in Kenya 117A.

The breeding behaviour of  $F_3$  and  $F_4$  lines confirms the conclusion drawn from  $F_2$  data.

TABLE 10.  
*The Breeding Behaviour of the Progenies of  $F_2$  Plants of the Cross Federation  $\times$  Kenya 117A Tested and Transplanted in the Field.*

	Seedling Reactions of $F_3$ Families to Race 222AB.			
	Resistant or Semi-resistant.	Segregating.	Susceptible.	Total.
$F_2$ seedling reactions to race 222AB:				
Resistant to semi-resistant .. ..	15	26	—	41
Susceptible .. ..	—	—	11	11
Total .. ..	15	26	11	52

P value for 1 : 2 : 1 ratio for  $F_3$  reactions lies between 0.70 and 0.80.

Some  $F_2$  seedlings from the resistant and susceptible classes were transplanted in the field. Their progenies were again tested with race 222AB to confirm the accuracy of  $F_2$  classification. The breeding behaviour of  $F_3$  families is correlated with the  $F_2$  reactions in Table 10.

As the resistance of Kenya 117A is dominant, the progenies of resistant  $F_2$  plants were either homozygous resistant or segregating, whilst all the susceptible  $F_2$  plants bred true in the  $F_3$  generation. The  $F_3$  test showed the correctness of the  $F_2$  classification.

In Tables 9 and 10, 75 segregating  $F_3$  lines of the cross Federation  $\times$  Kenya 117A consisted of 1375 plants of which 1009 were resistant to semi-resistant, 7 intermediate and 359 susceptible. By grouping the intermediate plants with the resistant ones, the data agree with 3:1 ratio with a P value of 0.30-0.50.

*Field Studies.*— $F_3$  plants of the cross Federation  $\times$  Kenya 117A were only moderately resistant in the field whereas Kenya 117A maintained its full resistance. One hundred and sixty  $F_3$  lines of the same cross were also grown and tested in the field for rust reaction to a mixture of four races of stem rust. The infection was good and Federation was severely rusted. The  $F_3$  lines were more difficult to classify and the segregation was not as clear cut as expected on the basis of a single dominant factor. Only 11 out of 160  $F_3$  lines approximated to the resistance of Kenya 117A. Some lines showed a range of reaction from resistance to moderate resistance and semi-resistance. Among the lines which segregated for resistance and semi-resistance were some that were difficult to separate from lines segregating for resistance and susceptibility. Likewise certain lines segregating for semi-resistance and susceptibility were hard to separate from homozygous susceptible lines. In such cases both the alternative classifications were recorded. The field reaction of  $F_3$  lines are given in Table 11 and are compared with the seedling reaction against race 222AB.

TABLE 11.

*Reaction of  $F_3$  Lines of the Cross Federation  $\times$  Kenya 117A in the Field and Their Relationship with the Seedling Reactions Against Race 222AB.*

	Field Reaction to Mixed Races.						Total.
	R.	R to R- or R to SR.	R and SR or R and S.	Seg.	SR and S or S.	S.	
Seedling reaction to race 222AB :							
Resistant to semi-resistant	11	12	13	3	—	—	39
Segregating .. ..	—	—	10	63	15	1	89
Susceptible .. ..	—	—	—	—	8	24	32
Total .. .. .	11	12	23	66	23	25	160

In cases when two alternative field reactions are given for  $F_3$  lines in Table 11, efforts were later made to find out the more probable ones. Of the 23 lines under the class R & SR or R & S, 17 were recorded as R to SR and 6 as segregating, and of the 23 lines under the class SR & S or S, 13 were recorded as susceptible and 10 as segregating. Taking the more probable reactions, 160  $F_3$  lines in the field can be classified as 11 resistant, 29 resistant to semi-resistant, 82 segregating and 38 susceptible. If the resistant and semi-resistant lines are treated as one class, the field data will fit 1:2:1 ratio with a P value of 0.90-0.95. The field reaction of  $F_3$  lines can be best explained by the presence of one main modifying factor and probably some minor genes which reduce the effectiveness of the gene for resistance in Kenya 117A in the mature plant stage. Except for the modifying factors, the seedling and the field reactions appear to show satisfactory correlation.

Table 11 shows that the resistant  $F_3$  lines, which all appear to be identical for their reaction in the seedling stage and are almost as highly resistant as Kenya 117A, show graded resistance in the field. Approximately  $\frac{1}{3}$  of the resistant and semi-resistant lines in the field or  $\frac{1}{16}$  of all the lines are almost as resistant as Kenya 117A. This is expected on the basis of the preceding explanation where one main modifying factor prevents the gene for rust resistance in Kenya 117A showing its full resistance in the field.

Clark and Smith (1935) reported the presence of modifying factors as it was difficult to obtain lines with as complete freedom from rust as the Hope and H-44 parents. Athwal (1953) reported modifying genes in crosses of Federation with Kenya 117A. Modifying factors probably also affect the field reaction of Kenya 744 as expressed earlier in this paper.

In backcrossing programmes carried out at Sydney University to incorporate the resistance of Kenya 117A into commercially desirable wheat varieties, it was found rather difficult to recover the full resistance of Kenya 117A.  $F_3$  lines from the successive backcrosses were necessary to insure that the complete resistance was present. Modifying factors can thus influence the breeding programme. If the full resistance is not obtained after the first backcross then it probably will not be recovered subsequently.

TABLE 12.  
*Reactions of  $F_3$ s and  $F_4$ s of the Cross Federation  $\times$  Kenya 117A Against Race 38.*

	Reactions to Race 38.				
	Resistant to Semi-resistant.	Intermediate.	Segregating.	Susceptible.	Total.
	Kenya 117A	—	—	Federation	—
$F_3$ s	236	13	—	12	261
$F_4$ s	69	—	90	9	168

*Relationship between races.*—Selected  $F_4$  lines of the cross Federation  $\times$  Kenya 117A were tested with races 126, 126B, 222AB and 222BB. All the 26 lines which were resistant and 25 lines which were susceptible to race 222AB behaved similarly with the other three races. Of the 12 lines which segregated with race 222AB as well as 126 and 222BB, 10 were found to be segregating against race 126B; one of the remaining two lines was resistant and the other susceptible. From the data it appears that the same gene in Kenya 117A gives resistance to all the races of stem rust in Australia.

TABLE 13.  
*Numbers of  $F_4$  Lines of the Cross Federation  $\times$  Kenya 117A Observed and Expected in Various Classes when Inoculated with Two Races of Rust.*

	Reaction to Race 222AB.			
	Resistant to Semi-resistant.	Segregating.	Susceptible.	Total.
Reaction to race 38:				
Resistant to semi-resistant	39 (40.5)	26 (20.25)	5 (10.125)	70 (70.875)
Segregating .. ..	—	65 (60.75)	18 (20.25)	83 (81.0)
Susceptible .. ..	—	—	9 (10.125)	9 (10.125)
Total .. ..	39 (40.5)	91 (81.0)	32 (40.5)	162

*Studies with race 38.*—Federation  $\times$  Kenya 117A  $F_3$ s were tested with race 38. Table 12 contains the data on  $F_3$ s and also a random sample of  $F_4$  lines of this cross.

If 13  $F_2$  plants showing intermediate type of reaction are grouped with the resistant class, the data will give a satisfactory fit to 15:1 ratio with a P value of nearly 0.30. The  $F_4$  data agree with 7.8:1 ratio with a P value of 0.50-0.70. Thus it appears that Kenya 117A also has two factors for resistance to race 38.

Reactions of 162  $F_4$  families of the cross Federation  $\times$  Kenya 117A to races 38 and 222AB are compared in Table 13.

In Table 13 all the lines that were resistant to race 222AB gave the same reaction against race 38. Of the lines that were segregating and susceptible with race 222AB, some bred true for resistance against race 38. It shows that one of the two factors in Kenya 117A for resistance to race 38 is the same as the one giving resistance to race 222AB and the other is independent of it. The figures within brackets in Table 13 indicate the number of lines expected on the basis of this hypothesis. The observed agrees with the expected with a P value of 0.30-0.50.

*Studies on the genetic relationship of the resistance of two Kenya wheats.*

F<sub>2</sub>s of a cross between Kenya 744 and Kenya 117A were tested with race 222AB in the glasshouse. All the plants were as resistant as the parents in the seedling stage and nearly as resistant in the field. F<sub>2</sub>s of a reciprocal cross also behaved in the same manner.

In the F<sub>2</sub> generation 1036 plants of the cross Kenya 744 × Kenya 117A and 380 plants of the reciprocal cross were tested with race 222AB in the glasshouse, but no susceptible segregate was found. Both the crosses showed segregation for mildew reaction.

TABLE 14.

*Reactions of Kenya 744 × Kenya 117A F<sub>2</sub>s and Federation × Kenya 117A F<sub>2</sub>s to Race 122.*

Cross and Generation.	Reactions to Race 122.			
	Resistant to Semi-resistant.	Segregating.	Susceptible.	Total.
Kenya 744 × Kenya 117A F <sub>2</sub> ..	Kenya 117A 355	—	Kenya 744 123	— 478
	Kenya 117A	—	Federation	—
Federation × Kenya 117A F <sub>2</sub> ..	37	93	35	165

P value for 3 : 1 ratio for the F<sub>2</sub> data lies between 0.70 and 0.80.—P value for 1 : 2 : 1 ratio for the F<sub>2</sub> data lies between 0.20 and 0.30.

Of the 1036 F<sub>2</sub> plants, 343 were transplanted in the field and their reactions to stem rust were recorded under conditions of heavy infection. The plants segregated for awn and other morphological characters. Whereas in the glasshouse the resistant reaction of all the plants was equal to the parents, in the field some plants showed moderate to semi-resistant and even intermediate type of reaction. A considerable amount of rust developed on the plants giving intermediate type of reaction but no fully susceptible plant was observed. The two parents maintained their resistance. Of the 343 F<sub>2</sub> plants in the field, 319 were as resistant or nearly as resistant as parents, 15 showed moderate to semi-resistance and 9 plants were intermediate for their reaction to stem rust. One hundred and thirty-one plants representing different field reaction (117 resistant, 10 moderately to semi-resistant and 4 intermediate) were harvested and their progenies tested with race 222AB in the seedling stage. All the 131 F<sub>3</sub> families bred true for resistance and they were all identical in their breeding behaviour in the seedling stage. The explanation for this is that the genes for resistance to race 222AB and consequently other Australian races are allelic in Kenya 744 and Kenya 117A. Modifying factors which are capable of influencing the field reaction of the two Kenya varieties are probably non-allelic.

As the gene for resistance to race 222AB in Kenya 744 and in Kenya 117A also gives resistance to race 38 no segregation for resistance to this race is expected in crosses between these two varieties. Such tests therefore will reveal nothing about the relationship of the second gene each of these wheats appears to possess against race 38. The reactions to different races of stem rust in Table 1, however, show that the two above varieties have at least one non-identical gene for rust resistance.

Kenya 744 is fully susceptible to races 122 and 24 at all temperatures tested, whereas Kenya 117A gives a reaction ranging from resistant to semi-resistant.  $F_2$ s of the cross Kenya 744  $\times$  Kenya 117A and  $F_4$  lines of Federation  $\times$  Kenya 117A were tested with race 122. The data in Table 14 show that a single dominant factor in Kenya 117A governs resistance to race 122 to which Kenya 744 is susceptible.

TABLE 15.  
*Numbers of  $F_4$  Lines of the Cross Federation  $\times$  Kenya 117A Observed and Expected in Various Classes when Inoculated with Two Races of Rust.*

	Reactions to Race 222AB.			
	Resistant to Semi-resistant.	Segregating.	Susceptible.	Total.
Reaction to race 122 :				
Resistant to semi-resistant	10 (10)	22 (20)	6 (10)	38 (40)
Segregating .. ..	21 (20)	51 (40)	19 (20)	91 (80)
Susceptible .. ..	8 (10)	15 (20)	8 (10)	31 (40)
Total .. ..	39 (40)	88 (80)	33 (40)	160

Reactions of 160  $F_4$  lines of the cross Federation  $\times$  Kenya 117A to race 122 and 222AB are compared in Table 15. The data show that the gene in Kenya 117A giving resistance to race 122 is quite independent of the gene for resistance against race 222AB. On the basis of independent segregation of the two genes in Kenya 117A, the breeding behaviour of  $F_4$  lines for reactions to races 122 and 222AB can be fitted with a ratio of 1:2:1:2:4:2:1:2:1. The figures in parenthesis in Table 15 show the calculated frequencies.

If the observed and the expected frequencies in Table 15 are compared, the P value lies between 0.50 and 0.70 indicating a good agreement.

TABLE 16.  
*Comparison of the Reactions of  $F_4$  Lines of the Cross Federation  $\times$  Kenya 117A to Race 122 and 38.*

	Reaction to Race 122.			
	Resistant to Semi-resistant.	Segregating.	Susceptible.	Total.
Reaction to race 38 :				
Resistant to semi-resistant	33	26	8	67
Segregating .. ..	3	67	19	89
Susceptible .. ..	1	—	7	8
Total .. ..	37	93	34	164

Koala is one of the varieties being used at Sydney University to incorporate the resistance of Kenya 117A into a commercially desirable genotype. Koala is susceptible to race 122 and 222AB. Sixteen families of the cross Koala<sup>2</sup>  $\times$  Kenya 117A which bred pure for resistance to race 222AB, were tested against race 122. Of the 16 families, 4 were resistant, 3 segregated and 9 were found to be susceptible to race 122. This indicates that new strains incorporating the resistance of Kenya 117A to Australian stem rust races would not necessarily show as wide a resistance as Kenya 117A.

In Table 16,  $F_4$  lines of the cross Federation  $\times$  Kenya 117A are compared for their reactions to race 122 and 38.

It appears from the table that one of the two genes in Kenya 117A against race 38 is the same as the one giving resistance to race 122. One line in Table 16 which was semi-resistant to race 122 was recorded as susceptible to race 38. The reaction of this line could not be re-checked, but this discrepancy is believed to be a mistake probably due to the effect of high temperature at which the tests were carried out against race 38. Three lines which were resistant to race 122 but segregated with race 38 can be expected on the basis of chance. The remaining 160 lines fit the expected ratio of 4:2:6:1:2:1 with a P value of 0.30-0.50, which is satisfactory.

Of the two factors in Kenya 117A against race 38, one gives resistance to race 222AB and the other gives resistance to race 122. On this basis, if the reactions of  $F_4$  lines are known against race 122 and 222AB, their reactions to race 38 can be

TABLE 17.  
*Symbols for Genes Controlling Rust Resistance in Kenya Wheats.*

Variety.	Symbol Suggested.	Particulars.	Previous Symbol (if Any).	Other Varieties Known to Have the Same Gene.
Kenya 743.	Sr. Ka1	Controls resistance to race 126, 222AB, etc.	F (Watson, 1952).	Eureka, Kenya 1304 (RL1373 Minn. 2693), Sweden 1230, Kenya 1034, Kenya 1037, (Watson and Waterhouse, 1949).
Kenya 744.	Sr. Kb1	Controls resistance to races 126, 126B, 222AB, 222BB, 38, etc.	H (Watson, 1952).	Allelic with one gene in Kenya 117A—Sr. d (present paper). Kb1
	Sr. b Kc2	Controls resistance to race 38.		Allelic <sup>1</sup> to one gene in Kenya 745.
Kenya 745.	Sr. Kc1	Controls resistance to races 126, 126B, etc.	$K_1$ (Watson, 1943).	Kenya 1035, Kenya 1049, Kenya 1053, Gabo, Yalta, Kendee, Charter (Watson and Waterhouse, 1949).
	Sr. Kc2	Controls resistance to race 38.	$K_2$ (Watson, 1943).	Allelic <sup>1</sup> to one gene in Kenya 744.
Kenya 117A 1347.	Sr. d. Kb1	Controls resistance to races 126, 126B, 222AB, 222BB and 38.	I (Watson, 1952). Kd, Athwal, 1953.	Allelic with one of the genes in Kenya 744—Sr. Kb.1. (Present paper).
	Sr. Kd1	Controls resistance to race 38 and 122.		

<sup>1</sup>  $F_2$ s of the cross Kenya 744 × Kenya 745 did not show any segregation for susceptible plants against race 38.

predicted. Any line which is resistant to one or both of the races 122 and 222AB would be resistant to race 38. Lines which segregate against one or both races should also segregate against race 38. Only those lines would be susceptible to race 38 which show susceptibility to each of the other two races. The reactions of 156  $F_4$  lines of the cross Federation × Kenya 117A to races 122, 222AB and 38 showed the appropriate correlation.

It can be concluded that the second gene in Kenya 744 which gave resistance against race 38 but not race 122 or 222AB must be non-identical to the second gene in Kenya 117A which was operative against race 38 and 122 but not race 222AB. It is also probable that genes in Kenya 744 and Kenya 117A governing resistance to four races of Australian stem rust are identical.

*Designation of Genes for Stem Rust Resistance in Kenya Wheats.*

Ausemus et al. (1946) proposed the symbols Sr. 1, Sr. 2, etc., for genes responsible for resistance to stem rust. These workers also recommended that a letter subscript, preferably the first letter of the variety, be used as a temporary designation for the factors until they can be checked against previously established ones.

Kenya wheats have contributed several non-allelic genes for resistance to stem rust. Taking into consideration the recommendations of the Committee on Nomenclature



of Genetic Factors (Ausemus et al., 1946), the writers suggest that these genes be designated according to the following scheme. K would show that the gene had first been found in a wheat from Kenya, letters a, b, c, etc., would indicate varieties within these introductions, and the subscripts 1, 2, 3, etc., would represent different loci when more than one is known in a variety. Where sufficient evidence is not available at present about allelic genes being identical, alphabetical superscripts will be used. According to this scheme the genes so far identified in Kenya wheats are listed in Table 17.

#### SUMMARY AND CONCLUSIONS.

Kenya 744 and Kenya 117A were each found to have a single dominant gene for resistance to 126, 126B, 222AB and 222BB races of stem rust. A satisfactory correlation was observed between the seedling and mature plant reaction to these races in crosses of Federation with these varieties, but resistance in the field appeared to be influenced by modifying factors.

Two dominant factors in Kenya 744 and in Kenya 117A governed resistance to race 38. One factor for race 38 in each of these two varieties was the same as giving resistance to races 126, 126B, 222AB and 222BB. The second factor in Kenya 117A also gave resistance to race 122 to which Kenya 744 was susceptible. It can be concluded, therefore, that the second factor in Kenya 117A is genetically different from either of the two factors in Kenya 744.

Kenya 117A is a variety having resistance to wheat stem rust over a wide geographical area. The genetical studies herein reported give some evidence that independent genes may operate to give resistance against races in those different areas. The gene present in this variety which is operative against the Australian rusts is allelic with the one present in Kenya 744 and is probably identical with it.

Since the second gene present in Kenya 117A and that in Kenya 744 are of no use against the Australian rusts these genes can be disregarded for wheat breeding purposes in this country.

The genetical similarity between these two rust resistant parents enables us to predict that, if a new race of rust occurs in Australia capable of attacking either Festival or Dowerin, the lines drawing their resistance from Kenya 117A will also be attacked. It is doubtful whether both varieties should be used concurrently in programmes to obtain stem rust resistant varieties.

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MACADAMIA TERNIFOLIA F. MUELL. AND A RELATED NEW SPECIES.

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*Synopsis.*

The two chief economic species of the Proteaceous genus *Macadamia*, "Queensland Nut", have been much confused in the past. The distinctions between these are worked out and it is shown that the correct name for one is *M. ternifolia* whereas the other, hitherto undescribed, is now named *M. tetraphylla*.

There are in cultivation two common species of *Macadamia* (Proteaceae), both known under the names of "Queensland Nut", "Popple Nut", and variants of the latter. These have been greatly confused, and misleading statements are common concerning the difference, or lack of it, between them. This has been due to several causes; firstly, semi-juvenile stages of one species resemble the mature stage of the other in the possession of toothed leaves; secondly, two states of the first species have been described under two different names; and thirdly, the second species has not been described or named at all.

The first species under consideration is the type species of the genus, *M. ternifolia* F. Muell., of which *M. integrifolia* Maiden & Betche is a synonym. This has toothed leaves in its earlier stages and often flowers in those stages, but in the fully mature stage the leaves are entire (whence the name *M. integrifolia*). This species is found in Queensland from Maryborough south to Beechmont and possibly in New South Wales, and various strains are cultivated. The second species, which has toothed leaves at all stages, has been wrongly known as *M. ternifolia* in New South Wales and overseas. It appears to grow naturally only on the far North Coast of New South Wales and the adjoining part of Queensland, but is also commonly cultivated. Those who know both species as living plants, calling the first *M. integrifolia* and the second (wrongly) *M. ternifolia*, have naturally been puzzled by statements (e.g. that of Francis, 1951, p. 91) to the effect that it is doubtful whether *M. integrifolia* is even varietally distinct from *M. ternifolia*. These statements are, however, technically quite accurate as made by those who have (correctly) applied the name *M. ternifolia* to dentate-leaved states of the first species.

The species may be distinguished as follows:

1. Leaves mostly in whorls of 4, always regularly spinose-dentate with about 35-40 teeth on each side, subsessile or on petioles not longer than 0.2 cm., lamina 7-25 cm. long,  $\pm$  truncate at the base, with 13-20 pairs of main lateral nerves. Inflorescence markedly loose-pubescent, often arising from older wood as well as new shoots, flowers somewhat purplish, seed surface somewhat wrinkled or with shallow depressions . . . . *M. tetraphylla*.
- 1\*. Leaves in whorls of 3 or sub-alternate, never in whorls of 4, in earlier stages irregularly spinose-dentate with up to 10 teeth on each side, in later stages entire, petiolate with petioles 0.4-1.5 cm. long, lamina 5-15 cm. long, tapered at the base, with 7-12 pairs of main lateral nerves. Inflorescence sparingly puberulous, usually near the ends of slender shoots, flowers cream, seed surface smooth . . . . . *M. ternifolia*.

MACADAMIA TETRAPHYLLA L. Johnson, sp. nov.

*Typification:* Lismore, N.S.W., T. G. Hewitt, IX.1909 (N.S.W. 25513), fl. HOLOTYPE.

Arbor mediocris staturae vel frutex altus, saepe multicaulis, cortice dense lenticellato. Ramuli verticillati, teretes dense lenticellati. Folia ramuli uniuscujusque superiora quaternata, infima opposita, media ternata, sessilia vel subsessilia (petiolis 0.2 cm. longis, brevioribusve) oblongo-oblongata, 7-25 cm. longa, 2.0-4.5 cm. lata, patentia, rigidiuscule coriacea, novella plus minusve colorata, glabra vel infra in costa

media praesertim sparsissime pilosa pilis fuscis vel pallidis perpauca, costa media prominens praesertim infra, pares nervorum primariorum lateralium 13-20, venuli coarctate reticulati et praesertim supra prominuli; apex laminae subacutus vel acutus, mucronatus, basis plus minusve truncata vel arcte contracta non sensim attenuata; margines semper regulariter antrorse spinoso-dentati dentibus utrinque 35-40, spinis 0.15-0.2 cm. longis.

Inflorescentiae axillares pseudoracemosae patentes vel subnutantes omnibus partibus pubescentibus, 12-30 cm. longae, rhachidis parte infima pedunculiforma 2-5 cm. longa. Bractee minutae caducae, irregulariter dispositae vel quasi-verticillatae, quaeque flores duos in pedicellis patentibus circiter 0.2-0.3 cm. longis subtendens. Perianthium pallide lilacinum 0.6 cm. longum extus pubescens, intus glabrum, limbo post anthesin revolutus; filamentorum pars libera circiter 0.025 cm. longa, antherae 0.1 cm. longae, pallidae, longitudinaliter dehiscentes; glandulae in discum cupuliformem coalitae; ovarium sessile villosulum, stylus cum ovario 0.8-1.0 cm. longus viride pallens infra pubescens supra glaber ad apicem anguste claviformis, stigma verum terminale minutum. Folliculus in pedicello brevissime crassiusculo, apiculato-globosus circiter 2.0->3.0 cm. diametro, glaber, paulo rugulosus, tarde dehiscent. Semen unicum apiculato-globosum, 1.5-2.0 cm. diametro, subfuscum vel laete castaneum, aliquanto nitidum, plus minusve rugosum vel laeviusculum, edule.

*Specimens examined.*—*Queensland*: Moreton District: Numinbah Valley, 2 miles south of Beechmont road turn-off, J. H. Beaumont, i.1954 (NSW. No. 26573), "furthest north of *M. tetraphylla* in this valley", fr.; Advancetown, Numinbah Valley, J. H. Beaumont, i.1954 (NSW. No. 26574), veg.; Natural Arch, Numinbah Valley, J. H. Beaumont, i.1954 (NSW. No. 26572), fr. *New South Wales*: North Coast: Near Mullumbimby, J. Farrell, 17.ix.1919 (NSW. No. 25504), fl.; Burringbar, Pope, ii.1897 (NSW. No. 25503), old inf.; Ballina to Bangalow, J. H. Maiden and J. L. Boorman, i.1903 (NSW. No. 25505), young fr.; Nimbin, E. Cheel, 13.ix.1926 (NSW. No. 25502), fl. buds; Lismore, Rothwell, xi.1906 (NSW. No. 25500), veg; Lismore, T. G. Hewitt, ix.1909 (NSW. No. 25513), fl., Holotype; Richmond River, — (NSW. No. 25506), fl.; Clarence River, — (NSW. No. 25501), fl.; without locality, — (NSW. No. 25507), fl. *Cultivated*: Botanic Gardens, Sydney, E. Betche, ix.1901 (NSW. No. 25508), "pink-flowering", fl., ix.1901 (NSW. No. 25509), "white-flowering", fl., L. A. S. Johnson, ii.1951 (NSW. No. 25512), "bushy shrub 12 feet, branching from base, fl. were mauve or pale lilac", fr.; Ashfield, E. Cheel, 28.x.1929 (NSW. No. 25511), veg.

The distribution of this species and the occurrence of hybrids are discussed under *M. ternifolia*. The maximum size of the species in its natural habitat, lowland rainforest or rainforest margins, is not known, though quite massive trunks are said to be formed. In cultivation it is often quite shrubby, several-stemmed from the base, and of densely bushy habit. The characters which distinguish it are given in the key above, and also under *M. ternifolia*. Variation in thickness of testa is notable, especially in cultivated plants. The flowers are usually pale lilac but occasionally pink or whitish. Occasional specimens are found, especially in cultivation, in which the leaves on most branches remain ternately rather than quaternately arranged, but these plants are absolutely typical in other respects and the ternate arrangement does not indicate hybridity unless accompanied by other intermediate features. On all such plants I have been able to find some shoots exhibiting the characteristic tetraphyllous condition.

This is the more common of the cultivated species in New South Wales, and in this State as well as in Hawaii it has been regarded as *M. ternifolia*. Mueller's type, however, and the *M. ternifolia* of Queensland botanists, is the following species.

MACADAMIA TERNIFOLIA F. Muehl.

In *Trans. Phil. Inst. Vict.*, ii, 1858: 72.

*Typification*: "In forests on the Pine River of Moreton Bay. Hill and Mueller." Part of this material, without precise indication of locality or collector is NSW. No. 25491 and agrees entirely with Mueller's plates (l.c.).

*Synonymy: Helicia ternifolia* F. Muell., *Fragm. Phytogr. Austral.*, II, 1860: 91; VI, 1868: 191. (As published in 1860 it was without any reference to *Macadamia ternifolia*, and though apparently based on the same material, was described as a new species.)

*Macadamia integrifolia* Maiden et Betche in *Proc. Linn. Soc. N.S. Wales*, XXI, 1897: 64. (Holotype: NSW. No. 25495, see below.)

*M. ternifolia* F. Muell. var. *integrifolia* (Maiden et Betche) Maiden et Betche, l.c., XXIV, 1899: 150.

Note.—The description given by Bentham, *Fl. Austral.*, V, 1870: 406, under *M. ternifolia* is based on material of both this species and *M. tetraphylla*. Many subsequent interpretations followed this.

The chief characters by which this species differs from *M. tetraphylla* are set out in the key above. Additional differences are the more slender, less prominently lenticellate branchlets, the usually greater breadth of the leaves proportional to their length, the paler coloration of young leaves, the occasional production of racemes on leafless shoots resulting in a compound inflorescence and the usually somewhat longer pedicels.

*Specimens examined.*—*Queensland*: Moreton District: See under Typification, above; Goonabah Creek, foot of Tamborine Mountain, W. Binsted per J. H. Beaumont, i.1954 (NSW. No. 26568), veg.; North Beech Mountain (Beechmont), J. H. Beaumont, i.1954 (NSW. No. 26570), "wild tree, in pasture (cleared rainforest)", veg.; The Pocket, Numinbah Valley, J. H. Beaumont, i.1954 (NSW. No. 26571), veg.; Beech Mountain, above The Pocket, J. H. Beaumont, i.1954 (NSW. No. 26569), "Furthest south that I have seen *M. ternifolia* in south-east Queensland", fr. *Cultivated*: Botanic Gardens, Sydney, E. Cheel, 20.viii.1925 (NSW. No. 25496), fl. buds, — x.1896 (NSW. No. 25497), fl. buds, —, xi.1896 (NSW. No. 25498), juvenile, L. A. S. Johnson, 5.ii.1954 (NSW. No. 26582), "bushy tree (single stem but branching low and stooling) 15–20 ft., infructescences pendulous, hidden among foliage. Young shoots not coloured." fr.; Oahu, Hawaiian Islands, H. M. Curran, No. 117, iv.1911 (NSW. No. 26687), fl.

*M. ternifolia*, like the preceding species, is found in lowland rainforest but its distribution is more northerly. At the present time plants are definitely known only as far south as the Numinbah Valley, north of the Macpherson Range. Dr. J. H. Beaumont states that he has not been able to find any plants of this species south of this area. However, the following specimens bear New South Wales localities: North Coast: Murwillumbah, Greer, iv.1931 (NSW. No. 25492), old infl.; Wilson's Creek, Richmond River, C. Moore No. 32, — (NSW. No. 25493), fl. buds; Lismore, R. White, x.1926 (NSW. No. 25494), fl.; Camden Haven, C. Moore? 1850–60 (NSW. No. 25495), fl.

Nos. 25492 and 25494 could well be from cultivated trees, but No. 25493 bears the note "plentiful" which would seem to indicate a natural occurrence, though Dr. Beaumont states that only *M. tetraphylla* is known in the Wilson's Creek district. This specimen has a few of its leaves in whorls of four and there is a suggestion that *M. tetraphylla* may have played a part in its ancestry, though it is much closer to *M. ternifolia* and certainly not a first generation hybrid. No. 25495 presents a problem since it is rather unlikely that the species would have been cultivated at Camden Haven at this early date. Possibly there was a confusion of localities by the collector. Camden Haven is much further south than any other known locality for either species.

*M. ternifolia* apparently attains a height of 70 feet or so under optimum conditions, but is frequently a much smaller plant, and often several-stemmed. The variability in leaf-dentition for which it is notorious seems to be largely a matter of physiological age. The toothed leaves are always quite different from those of *M. tetraphylla*. Occasional whorls of four leaves may be found in very young plants, but their occurrence in mature individuals is an indication of hybrid origin.

It seems very likely that *M. minor* F. M. Bail. (in *Queensl. Agric. Journ.*, XXV, 1910: 11) with which *M. lowii* F. M. Bail. (l.c., XXVI, 1911: 127) appears to be synonymous, is merely a local form or an ecotype of *M. ternifolia*, but field study is desirable to settle this point. I have seen the following specimen: Kin Kin, Queensland,

C. T. White, i.1916 (NSW. No. 25725), fr. This does not appear to differ significantly from many specimens of *M. ternifolia*.

HYBRIDS.—The following specimens are intermediate in all respects between *M. ternifolia* and *M. tetraphylla*. One group is found somewhat to the north of the known limit of the latter species and it is possible that *M. tetraphylla* has been "swamped" in that area by hybridization with *M. ternifolia*. The other group is from the known zone of contact of the two species. The specimens exhibit considerable variation which suggests the existence of a hybrid swarm, involving more than one generation of hybridity. The hybrids show intermediate conditions in petiole length, leaf shape and dimensions, number of marginal teeth and of lateral nerves, roughness of seeds and in general aspect. Flowers have not been seen. The number of leaves in the whorl is usually three, occasionally four. Variation on one plant may be considerable.

*Specimens examined.*—*Queensland*: Moreton District: Goonabah Creek, foot of Tamborine Mountain, W. Binsted per J. H. Beaumont, i.1954 (NSW. No. 26576), fr., (NSW. No. 26577), veg., (NSW. No. 26575), veg. [nearer *M. ternifolia*]; Walla Walla, Tamborine Creek, H. Welch per J. H. Beaumont, i.1954 (NSW. No. 26578), "old trees over 100 years old. 7 ft. in circumference at base of clump". fr.; Numinbah Valley, J. H. Beaumont, i.1954 (NSW. No. 26580), veg.; Beechmont (cult.), J. H. Beaumont, i.1954 (NSW. No. 26579), fr.

It is noteworthy that these hybrids are of restricted occurrence and that there is no general intergradation of the species which differ in a number of characters and are quite constant throughout their area, though apparently interfertile.

My thanks are due to Dr. J. H. Beaumont of the Hawaii Agricultural Experiment Station for renewing my interest in these two species of *Macadamia*, which are the basis of the Macadamia nut industry, and amongst the natural populations of which Dr. Beaumont is seeking promising plants for use in breeding and selection programmes.

*Reference.*

FRANCIS, W. D., 1951.—*Rain Forest Trees of Australia.*

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